Z. Säugetierkunde **64** (1999) 363–370

http://www.urbanfischer.de/journals/saeugetier

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allosuckling behaviour in Ammotragus

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Receipt of Ms. 21. 12. 1998
Acceptance of Ms. 20. 08. 1999

Abstract

Allosuckling behaviour is investigated in a captive population of Saharan arrui (*Ammotragus lervia sahariensis*). Allosuckling attempts are sporadic and usually unsuccessful (75%). The age of alien calves is strongly related to the age of allomother calves, and small differences in age between them are associated with successful allosuckling attempts. Young calves are also more successful when attempting allosuckling, although they undergo the most aggressive responses by the allomother. On the other hand, the two adoption instances observed took place in newborn calves. Neither the sex of the calf nor his/her coefficient of relationship with the allomother has any influence on the success of allosuckling. A series of hypotheses is discussed in the light of the results obtained; such as mistaken identification of the mother, kinship and crowded captive conditions.

Key words: *Ammotragus*, ungulates, allosuckling, adoption, maternal investment

Introduction

Adoption has been reported in *Ovis* and *Capra* genera (Hersher et al. 1963; Gubernick 1980) characterized by strong mother-infant bonds (e. g. Schaller 1977; Gubernick, 1981; Romeyer et al. 1993). Non-offspring nursing has been observed occasionally in both domestic and wild sheep (Hass 1990; see also Rowell 1991); allosuckling behaviour reported in the bighorn, *Ovis canadensis* (Hass 1990) and roe deer, *Dama dama* (Birgersson et al. 1991); and both casual allosuckling and adoption are commonly considered to occur in the bison, *Bison bison* (McHugh 1958; Altmann 1963; Lott 1972), and water buffalo, *Bubalus bubalis* (Tulloch 1979; Murphey et al. 1991).

Whenever alloparental care refers to allosuckling, occasional or frequent, costs for the donor (allomother) rise considerably (see Clutton-Brock et al. 1989). Recently, Packer et al. (1992) showed that non-offspring nursing is increased by captivity and in mammalian species that have large litters. These authors also pointed out that in monotocous taxa (those typically giving birth to only one infant) allosuckling is generally rare and females tend to be less tolerant (Packer et al. 1992).

The present study analyses both allosuckling and adoption in an African ungulate, the Saharan arrui (*Ammotragus lervia sahariensis*), a monotocous species with only one twin birth every 4.4 singles (Cassinello and Alados 1996). The aim of this study is to clarify the incidence of allosuckling behaviour in an ungulate social group, attempting to determine whether it is related to mistaken identifications of the mother by the calf, or promoted by either kinship or crowded conditions.

0044-3468/99/64/06 – 363 $ 12.00/0

Material and methods

Data were collected in a captive population of Saharan arrui which is successfully breeding in captivity at the Estación Experimental de Zonas Aridas (EEZA), Almería, south of Spain (Cassinello and Alados 1996). This population originates from just one male and one female captured in 1975 in the western Sahara. It is suspected that the subspecies is already extinct in the wild (Alados and Vericad 1993). Sampling was carried out from 1990 to 1992 in a herd made up of 17 males and 26 females at the beginning of the study, and 33 males and 43 females at the culmination of the study. The total surface available to the animals was 950 m^2. Detailed information on sampling method and routine can be found in Cassinello (1996), although a general description has been added here.

The animals were identified by means of coloured plastic ear tags, the differing position and shape of these tags determined a number for each individual. Birth date, parturition type (single or twin), sex, identity of father and mother, and inbreeding coefficient were known for each individual. Sampling was carried out during evenings, when females and calves were more active and the great majority of suckling events took place. Focal sampling was used to record mother and calf behaviour (Altmann 1974; Martin and Bateson 1986), each sample being 20 min duration. A sampling period was the total number of focals carried out on a given day. Every female which gave birth during 1990 and 1991 was sampled four times a week during the calf's first two months of life; during the remainder of the lactation period (for the weaning process, see Cassinello 1997 a) sampling was carried out 1.5 times per week. All mother-calf interactions between them and the other group mates were recorded. Suckling events were sampled ad libitum. A total of 26 mother-calf pairs was sampled; 8 calves shared their nursing with a sibling and 18 were single.

Only allosuckling attempts directed towards lactating females were taken into account. For the sake of clarity, throughout this study a calf attempting a suckling event on a lactating female other than his/her actual mother is named an alien calf, and the lactating female an allomother. In relation to the females' responses to the allosuckling attempts, four behaviours were distinguished: aggression, withdrawal, no response and adoption. No response means the allomother did not react when faced with an alien calf's allosuckling attempt, but this lack of response did not imply a successful attempt, as it might fail due to other factors, such as the lack of alien calf's determination while the allomother is engaged in other activities, i. e. feeding; in addition on one occasion a wire fence prevented the alien calf (no. 192) from allosuckling. Also, successful attempts could be followed by allomother rejection (aggression or withdrawal) once she is aware of the alien calf's presence, which might occur a few seconds later, enough time to score a successful event.

The coefficients of relationship (c. r.) between alien calves and allomothers were calculated following Maciejowski and Zieba (1982). The social ranks were calculated for all the lactating females, and the rank given to a particular individual corresponded with the percentage of individuals with a lower dominance status (Cassinello 1995). When parametric tests were used, non-normal dependent variables were transformed according to, e. g., Zar, (1984). Replication was tackled by means of the analysis of intra and intergroup variance, which showed for all the response variables that the intergroup variance was not greater than the intragroup variance, so that all the data were considered as independent.

Results

Allosuckling, carried out by 10 different calves, occurred sporadically in the population under study: only 20 events were registered during the whole sampling period, two of them leading to adoptions (Tab. 1). Taking into account the first suckling attempt which led to an adoption as an allosuckling one, the percentage of occurrence of allosuckling behaviour was as follows: 3.3% of the whole suckling behaviour (20 out of 611 events registered), 1.4% of the successful suckling events (5 out of 357), and 5.9% of the unsuccessful ones (15 out of 254). Allosuckling took place at very different ages, from 0 to 463 days-old (Tab. 1), although the median is 19 days, and the mean 62 days (0 days refers to newborn individuals).

A strong and positive relationship between the age of alien calves and the age of allomothers' calves can be seen first (simple regression: $n = 20$, $r^2 = 0.51$, $P = 0.0004$; Fig. 1).

Table 1. Some characteristics of the allosuckling behaviour observed in the studied population. Response refers to the allomother's reaction against allosuckling attempts. Key: F = female, M = male, S = successful, U = unsuccessful, Adop = adoption, NR = no response, Agg = aggression, and W = withdrawal

Calf number	Calf sex	Allosuckling	Allomother no.	Response	c. r.
149	F	S	26	Adop	0.5759
153	F	S	46	Adop	0.5666
153	F	U	28	NR	0.5434
155	F	S	31	Agg	0.5206
155	F	U	31	W	0.5206
156	M	U	33	W	0.4900
157	F	U	35	W	0.4900
157	F	S	35	W	0.4900
186	F	U	28	Agg	0.6214
186	F	U	21	NR	0.6062
186	F	U	21	Agg	0.6062
186	F	U	26	W	0.5456
186	F	U	64	W	0.5259
188	M	U	17	Agg	0.5153
188	M	U	26	Agg	0.5911
192	M	U	26	Agg	0.5759
192	M	U	36	NR	0.5153
194	F	U	26	Agg	0.5206
194	F	U	21	NR	0.4900
195	F	S	28	Agg	0.5819

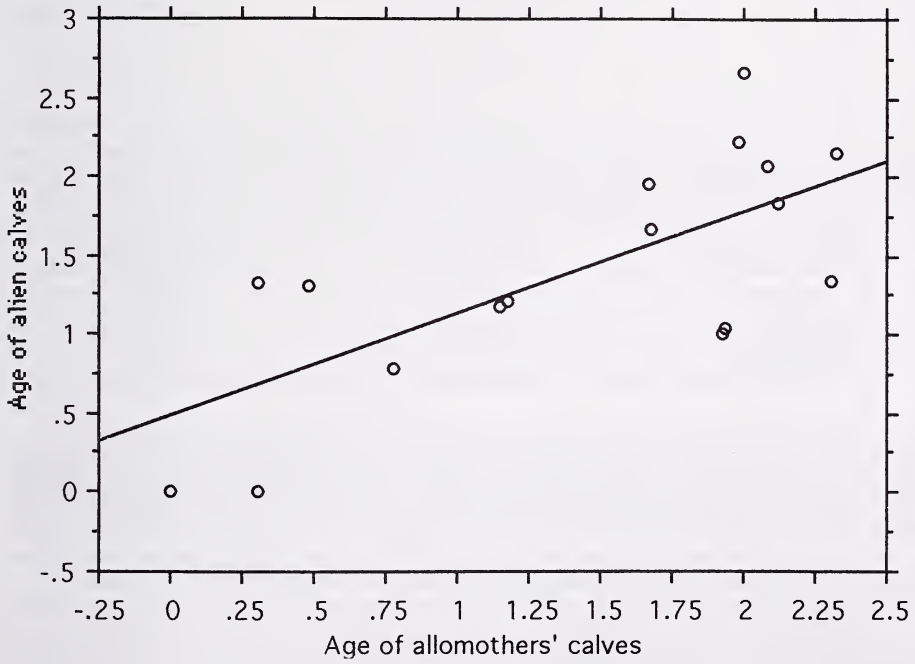

Fig. 1. Relationship between the age of alien calves and the age of allomothers' calves. Age shown is in days transformed into their logarithm to run the simple regression analysis.

However, no relationship was found between the age of alien calves and their coefficient of relationship with the allomothers ($n = 18$, $r^2 = 0.001$, $P = 0.89$).

The age of calves who successfully attempted allosuckling (25% of the total attempts) was lower than that of calves who performed unsuccessful allosuckling (successful calves: 8 ± 4 days; unsuccessful calves: 80 ± 30 days; ANOVA: $F(1.18) = 10.33$, $P = 0.005$); also, successful allosuckling was observed on mothers who were nursing younger calves (4 ± 2 days) than unsuccessful ones (77 ± 18 days; $F(1.18) = 11.00$, $P = 0.004$). Furthermore, the success of allosuckling was greater when the difference in age between alien calves and allomothers' calves was smaller (4 ± 3 vs 66 ± 25 days; $F(1.18) = 5.48$, $P = 0.03$). Neither the coefficient of relationship between alien calves and allomothers ($F(1.18) = 0.02$, $P = 0.89$) nor the allomothers' social rank ($F(1.18) = 1.66$, $P = 0.21$) had any influence on the success of the allosuckling attempts.

Both the mean age of the alien calves and the age of the allomother were significantly different for the four allomother's responses considered; the differences being particularly acute between calves actually adopted (newborn) and the remaining cases (see Tab. 2). The four types of responses showed similar values for the difference in age between alien calves and allomothers' calves ($F(3.16) = 0.88$, $P = 0.47$), and the coeficients of relationship between alien calves and allomothers ($F(3.16) = 2.93$, $P = 0.07$).

The allomothers' type of response varied depending on their social rank: withdrawals were carried out by low-ranking females (Tab. 3); on the contrary, neither the actual mother's rank nor the rank difference between mother and allomother was related to the latter's response (Tab. 3); although there is a tendency for allomothers of relatively low rank in relation to the actual mother's rank to withdraw when faced with calf's allosuckling attempts (Fisher's post-hoc test: $P = 0.06$).

A three-fourths majority of the calves who attempted allosuckling was females, but this number was not statistically significant (Fisher's Exact Test: $df = 1$, $P = 0.19$). Both males and females attempted allosuckling at the same average age ($F(1.18) = 0.11$,

Table 2. Mean ($\pm$SE) age in days of both alien and allomother's calf in relation to the response of the allomother to the allosuckling attempt. [a]ANOVA: $F(3.16) = 7.15$, $P = 0.003$; Fisher's post-hoc test: aggression vs no response $P = 0.05$, adoption vs the others $P < 0.004$. [b]ANOVA: $F(3.16) = 4.39$, $P = 0.02$; Fisher's post-hoc test: adoption vs aggression $P = 0.008$, adoption vs no response $P = 0.007$.

Allomother's response	Alien calf age[a]	Allomother's calf age[b]
Agression	28.5 ± 11	72 ± 24
Withdrawal	58 ± 27	37.5 ± 22
No response	166 ± 102.5	92 ± 43
Adoption	0	0.5 ± 0.5

Table 3. Mean ($\pm$SE) mother's rank, allomother's rank, and ranks difference in relation to the response of the allomother to the allosuckling attempt. [a]ANOVA: $F(3.16) = 0.91$, ns. [b]ANOVA: $F(3.16) = 4.20$, $P = 0.02$; Fisher's post-hoc test: aggression vs withdrawal $P = 0.007$, withdrawal vs no response $P = 0.02$. [c]ANOVA: $F(3.16) = 1.63$, ns.

Allomother's response	Mother's rank (A)[a]	Allomother's rank (B)[b]	(A–B)[c]
Agression	58 ± 9	79 ± 4	-21 ± 12
Withdrawal	64 ± 6	53 ± 6	11 ± 7
No response	58 ± 11	80 ± 9	-21 ± 19
Adoption	36 ± 3	56 ± 16	-20 ± 13

P = 0.74). No relationship was found between the sex of the alien calf and the coefficient of relationship with the allomother ($F(1.18) = 0.17$, $P = 0.68$). Finally, the success of the allosuckling behaviour (Fisher's Exact Test: $df = 1$, $P = 0.27$) and the allomother's responses (Contingency table: $df = 3$, $\chi^2 = 1.56$, $P = 0.67$) were not influenced by the sex of the alien calf.

Only once did a permanent adoption event happen in the study population, where a female (no. 26) allosuckled an alien female calf (no. 149) from birth to her premature death. Just after birth, calf no. 153 was unusually adopted during one day by female no. 46; but eventually the allomother stopped nursing the calf which was then nursed by her actual mother (no. 64). Female no. 46 had deserted her twins (calves no. 148 and 149) just after birth, and one of them (no. 148) was killed by female no. 64. Both adoption events happened to female calves whose age was significantly lower than that of the calves which attempted allosuckling ($F(1.18) = 14.93$, $P = 0.001$). The coefficients of relationship with the allomothers were slightly higher in the adoption cases (0.57 ± 0.005 vs 0.54 ± 0.01), but the difference was not statistically significant ($F(1.18) = 0.84$, $P = 0.37$). Finally, social ranks of adoptive mothers did not differ statistically from those of non-adoptive mothers ($F(1.18) = 0.77$, $P = 0.39$).

Discussion

Casual allosuckling has already been reported in *Ammotraus* by Katz (1949) and Haas (1959), and is considered to occur occasionally in ungulates (e. g. Hass 1990). In the study population, a strong relationship is found between the age of alien calves and the age of allomothers; successful allosuckling attempts depending on this relationship. Moreover, young alien calves are more successful when attempting allosuckling; this might be related to an inefficient sort of "labelling" (sensu Gubernick 1980) or the mother's ability to memorize their own calves' signatures (Porter et al. 1991; but see Romeyer et al. 1993); thus, arrui mothers would recognize older calves more easily. Also the older calves' behaviour might account for these results.

Captivity conditions might promote a certain permissive behaviour towards alien infants, as the mothers have unlimited access to food and the costs associated with nursing are diminished (see Packer et al. 1992); also overcrowding conditions may favour this sort of behaviour (Riedman 1982). But, on the other hand, in social herbivores alien calves are usually rejected by females, a behaviour which is expected to be favoured by natural selection (Gubernick 1981; Harper 1981) unless some sort of benefits came along with allomothering, such as those related to kinship selection (Bertram 1976). Furthermore, recent evidence on monotocous mammalian species, where most social herbivores are included, seems to show that they are poorly tolerant of allosuckling behaviour (Packer et al. 1992).

Calves' mistaken identification of their own mothers may be an explanation for allosuckling to occur, although in some instances single alien calves (not used to share suckles) attempted allosuckling when the allomother's own calves were already suckling. Also, allosuckling attempts might be part of calves' learning behaviour, which may be implemented through negative responses.

A rather speculative hypothesis which might explain the origin of this behaviour refers to young arrui calves seeking extra-milk intakes from lactating females other than their mothers, when young calves of similar ages can be mistaken by adult females; thus, the allosuckling behaviour may well be pursued by alien calves to obtain an additional source (Murphey et al. 1991); however, not enough data are available to test this hypothesis.

On the other hand, allomothers' responses against casual allosuckling were particularly aggressive when addressed to young calves; this may indicate that they represent a more serious threat to maternal resources than older calves, perhaps due to their more efficient suckling behaviour (Cassinello 1996). Also, the hypothetical source of error commented above may provoke this strongly agonistic response. Allomothers who displayed the most submissive response (withdrawal) held the lowest social ranks; but the scarcity of data available does not permit any conclusion on this matter.

The lack of any relationship found between the coefficient of relationship and the allosuckling behaviour in the study population of Saharan arrui might be explained by the high inbreeding coefficients that characterize this population (e. g. Cassinello 1997 b), which causes a low variance for this coefficient (c. r. range = 0.13; minimum value = 0.49; maximum value = 0.62). On the other hand, familiarity might also play an important role in the allomother's tolerance towards alien calves (D'Amato 1993), but we have no data yet to support or refute such a hypothesis. It has been found in sheep that even with a high degree of familiarity (i. e. dizygotic twins), mothers can discriminate between lambs; and familiarity tended to reduce the rejection of a twin kept separated from its mother when compared with a totally alien lamb (Romeyer et al. 1993).

The low frequency of occurrence of casual allosuckling behaviour raises the question of costs and benefits to both alien calves and allomothers. It might be postulated that costs to the calf in terms of aggression, chasing, etc. tend to exceed the benefits obtained (milk intake); although no direct measure of such costs/benefits is available.

As for the adoption events observed in the study population, the high degree of relatedness between all of the individuals makes an explanation in terms of kinship selection unsatisfactory. Hass (1990) reported alloparental behaviour in bighorn females which had lost their lambs 3–40 days after parturition, and Rowell (1991) referred to a similar case in sheep. Probably these lactating females were physiologically and behaviourally "primed" for lactation (Oftedal 1985). A painful, distended udder may be the impetus for nursing alien calves, although it cannot explain why these females continue to nurse calves for the entire lactation period (Hass 1990). Moreover, in sheep, as in other mammals (see Gubernick and Klopfer 1981), there appears to be a sensitive period following parturition during which ewes will be responsive to all lambs, since ewes separated from their lambs at birth will still show maternal behaviour towards any lamb within 4–8 h postpartum (Smith et al. 1966; Poindron et al. 1979). In addition, and although Gubernick's (1980) labelling hypothesis has been questioned recently (Romeyer et al. 1993), maternal attachment in ungulates may take some time for the mothers to discriminate between their own and alien calves. In the studied Saharan arrui population, the adoptees were always newborn calves, while the allomothers had just given birth. Allomothers had not lost their calves before adoption took place, so Oftedal's (1985) hypothesis cannot apply here. The adoptees were deserted by their own mothers a few minutes after birth, although in the one-day adoption this abandonment persisted for only one day.

Recently, a new controversy has arisen concerning a hypothetical transmission of phenotypic characters by means of adoption (Avital and Jablonka 1994, 1996; Hansen 1996). In the Saharan arrui, no benefits, in terms of acquiring a higher social status, were observed (Cassinello 1995) during the actual adoption event; moreover, the allomother had to allocate her resources towards the adoptee and her own calf. In sum, the one-day adoption observed might be considered as a temporal allomother's mistake or even tolerance, and the long-lasting adoption might have been provoked by the overcrowding conditions (Riedman 1982) or by the abandoned alien calf which managed to take advantage of a lactating female who had just given birth (Smith et al. 1966).

In conclusion, evidence of allosuckling behaviour in *Ammotragus* is provided, and possible adaptive interpretations postulated.

Acknowledgements

Thanks go to T. Abaigar, M. Gomendio, and two anonymous referees for constructive comments on earlier versions of the manuscript, and to Juan Moreno for translating the abstract into German. During data collection the author enjoyed a predoctoral grant from MEC (PG89 27511603), being currently supported by DGES Project PB96-0880.

Zusammenfassung

Fremdsaugen bei Ammotragus

In einer in Gefangenschaft gehaltenen Population des Mähnenspringers (*Ammotragus lervia sahariensis*) wurde die Milchaufnahme von Kälbern bei fremden Müttern untersucht. Derartige Saugversuche sind selten und gewöhnlicherweise nicht erfolgreich (75%). Das Alter der fremden Kälber ist dem der eigenen Jungtiere ähnlich, doch geringe Altersunterschiede steigern den Erfolg bei Fremsaugaktivitäten. Wenn auch junge Kälber besonders aggressive Reaktionen der fremden Mutter hervorrufen, so sind sie doch bei ihren Versuchen besonders erfolgreich. Es wurden zwei Fälle von Adoption gerade bei neugeborenen Kälbern beobachtet. Weder das Geschlecht, noch der Grad der Verwandtschaft mit der Fremdmutter beeinflussen den Erfolg der Jungtiere bei der Nahrungsaufnahme an fremder Quelle. Im Lichte der erhobenen Befunde werden mehrere Hypothesen diskutiert: Fehl-Identifikation, Verwandtschaft und hohe Populationsdichte in der Gefangenschaft wurden berücksichtigt.

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